BIG IDEAS:

- Ecologists use species richness and relative abundance to measure and compare biological communities.
- Biodiversity refers to the variety of genes, species and ecosystems in a given area.
- Biodiversity is affected by latitude, habitat complexity and area.
- The species richness of a community is a balance between immigration and extirpation.
- Communities undergo a sequence of predictable changes following a disturbance.
- Early and late successional species have different adaptations.

DIVERSITY AND DISTURBANCE OF Biological Communities

In seconds, the chainsaw chewed through 70 years of growth. When he saw the massive oak begin to lean, the logger stepped nimbly to one side. Gravity finished the job, pulling three tons of tree to a limb-snapping, ground-shuddering finish.

For the lumberjack, it was just another day of logging at Peck Ranch Conservation Area. For the ecologist watching nearby, it was the beginning of an unprecedented study. Unlike most ecological studies, which typically span two or three years, the Missouri Ozarks Forest Ecosystem Project is scheduled to run for 100 years.

Work on this project began in 1991 when crews of ecologists, conservationists and college students scoured 3,700 hectares of Ozark forest to gather baseline data. Crews tallied trees in the canopy, counted plants in the understory and inventoried insects crawling on the forest floor. Some crews focused on amphibians, birds and mammals. Others measured abiotic components of the forest, such as soil types and climate. All this information painted a detailed portrait of the forest at a particular point in time.

With that snapshot in their photo album, researchers began harvesting trees in different parts of the forest. In some areas, all the trees were cut. In other areas, some trees were cut while others were left standing. In still other areas, no trees were cut at all.

Over the next ten decades, scientists will gather terabytes of data about how organisms react to these harvests and others yet to come. Their work will add volumes to what we currently know about the structure and function of biological communities. In this chapter, we will learn how ecologists measure and compare communities, investigate factors that affect the number and variety of organisms making up a community, and explore how communities change over time.

A forest community is shared by many coexisting populations.

Ecologists use species richness and relative abundance to measure and compare biological communities.

Every place on earth—each marsh, each prairie, each leaf at the tip of a white oak—is shared by many coexisting populations. They form what ecologists refer to as a **biological community**, a group of populations that live and interact in the same place at the same time. Organisms within a community are linked together by the flow of energy in food webs and the cycling of elements. Organisms compete with, exploit and help each other. In doing so, they affect the size of their own population and other populations.

Even the simplest biological communities contain overwhelming numbers of species. A handful of dead leaves collected from an Ozark forest might contain more than 65 different kinds of insects, spiders and mites, not to mention hundreds of different microscopic fungi, protists and bacteria. In addition, the movements of animals, seeds and organic material link biological communities together, making it nearly impossible to determine where one community ends and another begins. To manage this complexity, ecologists often study subsets of biological communities, focusing, for example, on the plant community in a 9,000-hectare forest, the fish community in a kilometer of the Jack's Fork River, or the insect community living in a single bur oak.

Ecologists study a community's **structure**, the living organisms it is composed of, and **function**, how those organisms interact to sustain the community. One of the most revealing measures of a community's structure is the number of species it contains. Ecologists call this measurement **species richness**.

Imagine sampling the tree species in one hectare of Ozark forest. Each time we encounter a new kind of tree, we record it on a data sheet. When we've finished sampling, we have recorded the tree species listed in the first column of Table 8.1. To determine the species richness of our sample, we simply count the number of

Species	Number of Individuals	Percentage
Scarlet oak	63	25.00%
Black oak	38	15.00%
Hickory	20	8.00%
White oak	20	8.00%
Flowering dogwood	18	7.00%
Shortleaf pine	16	6.50%
Red maple	15	6.00%
Eastern red cedar	13	5.00%
White ash	10	4.00%
Wild cherry	10	4.00%
Sycamore	10	4.00%
Cottonwood	8	3.00%
Sassafras	8	3.00%
American elm	3	1.00%
American basswood	1	0.50%
TOTAL	250	100.00%

Table 8.1—Species Richness and Relative Abundance of Trees in an Ozark Forest

species we have recorded, in this case, 15. Species richness, however, describes only part of a community's structure. To obtain the full picture, we need to count how many individuals of each species are in our sample area. This measurement, shown in the second column of Table 8.1, is called **relative abundance** or **species evenness**. Relative abundance shows how *abundant* one species is *relative* to all the others in a community. It is often expressed as a percentage. In our sample, scarlet oak has a relative abundance of 25 percent of the trees, while American basswood has a relative abundance of less than 1 percent.

When we look closely at Table 8.1, an interesting pattern emerges. We see that a few species, such as scarlet oak and black oak are extremely abundant. We also notice that a few species, such as American elm and basswood, are extremely rare. The majority of trees—everything from hickory to sycamore—are moderately abundant. If we were to plot this on a graph, it would show a bell-shaped curve similar to Figure 8.1. Nearly all communities show this pattern of relative abundance. Whether we sample trees in an Ozark forest or fish in an Indonesian coral reef, we would find that most species are moderately abundant, while few are very abundant or extremely rare.

Ecologists have found that the more you sample a specific community, the more species you will find. Common and abundant species turn up in small samples, but a great deal of effort and a large sample is needed to find the rarest species. As a result, only large samples produce a full bell-shaped curve.
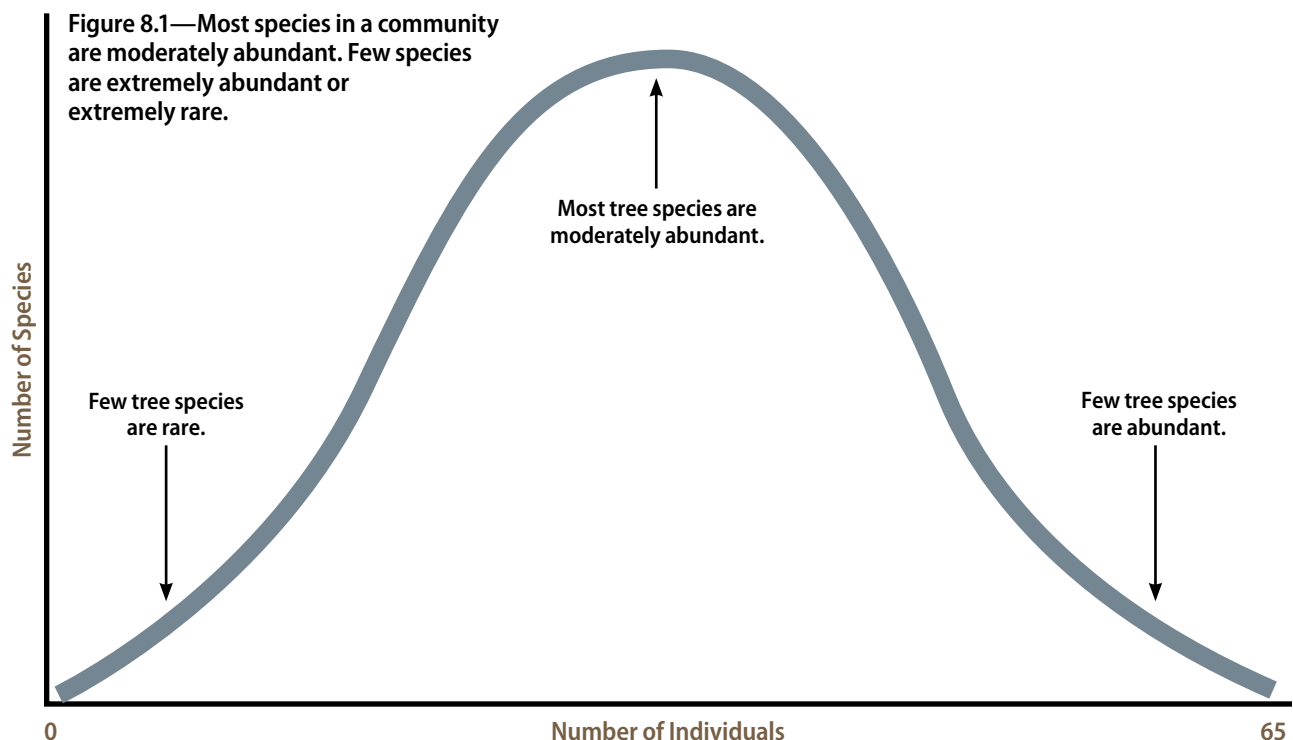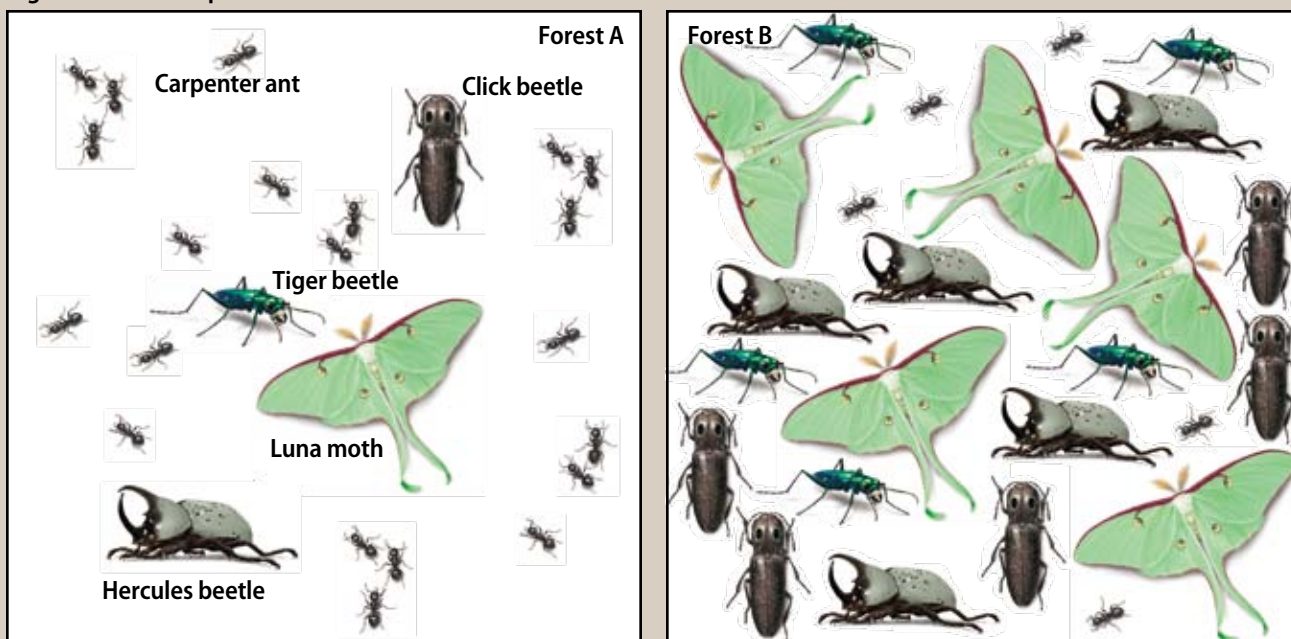

Figure 8.1—Most species in a community are moderately abundant. Few species are extremely abundant or extremely rare.

Most tree species are moderately abundant.

Few tree species are rare.

Few tree species are abundant.

Number of Species

Number of Individuals

0   65

Figure 8.2—A Comparison of Insect Communities in Two Forests

Taken together, species richness and relative abundance give an impression of the variety of life that exists in a community. To illustrate the relationship between species richness and relative abundance, let's compare the insect communities in two different forests *(Figure 8.2)*.

Both forests contain five different insect species, so they have equal amounts of species richness. In Forest A, however, carpenter ants have a relative abundance of 84 percent, while each of the other insect species makes up only 4 percent of the community. In Forest B, all five species are equally abundant, each making up 20 percent of the community. If we were to walk through each forest, we would probably notice that Forest B seems to have more variety than Forest A. Ecologists use **diversity indices** to quantify this impression.

A commonly used diversity index is the Shannon-Wiener index. Here's the equation:

$$H' = - \sum p_i (\log_e p_i)$$

H'	=	the value of the Shannon-Wiener index
p_i	=	the proportion of each species
$\log_e$	=	the natural logarithm

Don't let this equation scare you! A Shannon-Wiener index isn't hard to calculate once you know how to do it. Just follow these steps:

1. Determine the proportions of each species in the community. To do this, take the number of individuals in one species and divide by the total number of individuals in the entire sample. There are 21 carpenter ants in Forest A and 25 total individuals in Forest A. Thus, 21 ÷ 25 = 0.84. Do this for every species.
2. Multiply each proportion from step 1 by its natural logarithm. A scientific calculator comes in handy, here. For carpenter ants, type 0.84 into your calculator and push the key marked "ln" or "$\log_e$." You should get a value of -0.174. Do this for every species.
3. Multiply the proportion for each species by the value you calculated in step 2. For carpenter ants we would multiply 0.84 by -0.174 for a value of -0.146. Do this for every species.
4. Add together each of the values from step 3. For the species in Forest A, we would calculate this value like this: -0.146 + -0.129 + -0.129 + -0.129 + -0.129 = -0.662.
5. The number you arrive at in step 4 will be a negative number. The Shannon-Wiener index calls for taking its opposite. Thus, -0.662 becomes 0.662.

Forest A

Species	Number	Proportion (p_i)	$\log_e p_i$	$p_i \log_e p_i$
Carpenter Ant	21	0.84	-0.174	-0.146
Luna Moth	1	0.04	-3.219	-0.129
Tiger Beetle	1	0.04	-3.219	-0.129
Click Beetle	1	0.04	-3.219	-0.129
Hercules Beetle	1	0.04	-3.219	-0.129
TOTAL	25	1.00		-0.662

H' = 0.662

Forest B

Species	Number	Proportion (p_i)	$\log_e p_i$	$p_i \log_e p_i$
Carpenter Ant	5	0.20	-1.609	-0.322
Luna Moth	5	0.20	-1.609	-0.322
Tiger Beetle	5	0.20	-1.609	-0.322
Click Beetle	5	0.20	-1.609	-0.322
Hercules Beetle	5	0.20	-1.609	-0.322
TOTAL	25	1.00		-1.610

Table 8.2—The Shannon-Wiener index has been calculated for Forest A (top) and Forest B (bottom). Notice that Forest B has a higher index and, therefore, more species diversity.

H' = 1.610

In a community with one individual, H' (the Shannon-Wiener index) would be 0. The value of H' increases as species richness and relative abundance increase. Thus, higher values of H' indicate more variety or **species diversity** in a community. Table 8.2 calculates the Shannon-Wiener index for our two insect communities. You'll notice that Forest B has a higher index. This is because the relative abundance of the insects in Forest B are more evenly distributed.

Biodiversity refers to the variety of genes, species and ecosystems in a given area.

Missouri is a biological melting pot. Within our state's borders roam about 70 different kinds of mammals, more than 400 species of birds, and over 100 species of amphibians and reptiles. No region of the world has a more diverse mix of freshwater fishes—nearly 200 species cruise our state's streams, rivers and lakes. An estimated 18,000 different kinds of insects flutter, buzz, burrow, swim and scurry through Missouri. More than 20 different kinds of oak trees help make up over 2,500 different kinds of plants that grow here. New species turn up every year.

Ecologists have barely recorded all the plants, animals and fungi that live in Missouri, let alone throughout the world. Nearly 1.5 million species have been described and named worldwide. Ecologists estimate that more than 10 million species likely exist on Earth *(Figure 8.3)*. These species make up the biological diversity, or **biodiversity**, of our planet. Biodiversity is made up of three components:

- Species diversity refers to the species richness and relative abundance found in a certain area.
- Genetic diversity is the variety of genotypes found among individuals in a population. This is a critical component of biodiversity, because, as we learned in chapter two, high genetic diversity allows a species to adapt to changing environments.
- Ecosystem diversity refers to the variety of different ecosystems that exist within a larger region such as a landscape or watershed.

Biodiversity is often used to mean species richness. Regardless of how precisely the term is used, biodiversity offers an important yardstick to measure and compare different biological communities. This helps ecologists determine which areas support the greatest number of species, which areas would make good nature preserves, and which areas might provide habitat for rare or endangered species.
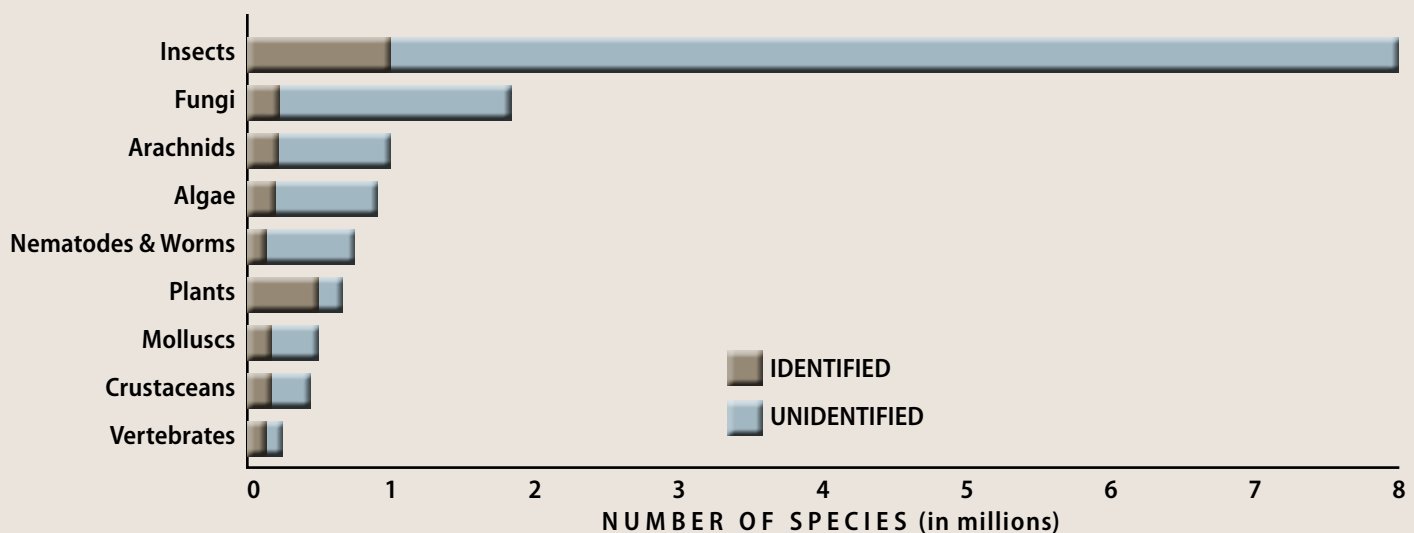
Figure 8.3—Estimated Worldwide Species Richness for Various Groups of Organisms
(Data from Millennium Ecosystem Assessment, 2005, World Resources Institute)

Species in a community interact with and depend upon each other in many ways. As a result, the loss of one species can bring about the loss of others. High biodiversity helps stabilize biological communities and helps communities recover from environmental change or human disturbance. Ecologists have shown that ecosystems—whether forests, prairies or wetlands—recover faster from droughts, fires, diseases and other natural disasters if they harbor many species rather than just a few. This is why preserving areas of high biodiversity has become a priority for conservationists throughout the world.

Before European settlement, Missouri's biodiversity remained relatively stable for thousands of years. Over the last two centuries, however, human activity has drastically altered our state's biodiversity. During this time, we have destroyed habitats, introduced invasive species and hunted other species to the point of extinction. Our history is mirrored by what is happening worldwide. As many species become rare or extinct—some even before they've been cataloged by scientists—ecologists feel an urgent need to understand why some communities have more biodiversity than others and find ways to preserve as many species as possible.

## Biodiversity is affected by latitude, habitat complexity and area.

Different areas—even areas separated by just a few hundred meters—may vary greatly in the number and variety of species that live there. On the northeast side of an Ozark hill, we might find plants and animals adapted to shady, relatively wet conditions, such as white and red oaks, shortleaf pines, flowering dogwoods, tiger salamanders, pileated woodpeckers and flying squirrels. If we were to walk over the ridge to the southwestern side of the hill, we would likely find animals adapted to sunnier and drier conditions. Here we might encounter grasses, such as little bluestem, Indian grass and sideoats grama, collared lizards, roadrunners and scorpions *(Figure 8.4)*. This raises an important question: Why do communities differ in the biodiversity they contain?

On a local scale, differences in the number and variety of species occur because different areas have different abiotic conditions. Because it is shaded from hot afternoon sunshine, the northeastern side of an Ozark hill has lower temperatures and lower evaporation rates than the southwestern side. Thus, the abiotic properties of a northeastern hillside meet the niche requirements of organisms adapted to cooler, wetter and shadier conditions. Likewise, the abiotic properties of the southwestern hillside satisfy the niche requirements of organisms adapted to hotter, drier and sunnier conditions.

Figure 8.4—On a local scale, species diversity is affected by differences in the abiotic conditions from one area to another. For example, organisms on north-facing slopes are adapted to shadier, cooler and wetter conditions, while organisms on south-facing slopes are adapted to sunnier, hotter and drier conditions.

Forest

Glade

Woodland

← South facing slope | North facing slope ➡
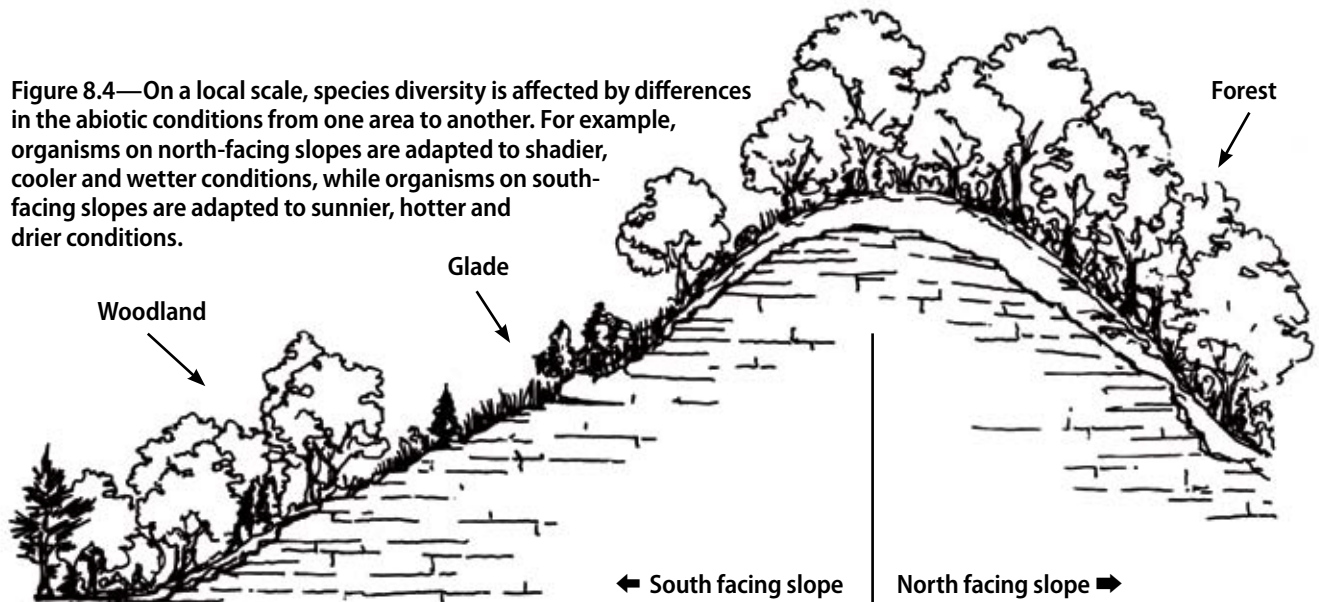
If we examine biodiversity on a regional or global scale, other patterns emerge. Explorers and naturalists of the 19th century, including Charles Darwin and Alfred Wallace, were astounded by the vast array of life they found in the tropics. A century later, ecologists began to compare species richness in the tropics to other latitudes. They found that with most groups of organisms—from mammals to microbes—species richness increases toward the equator. For example, the boreal forests of Manitoba, Canada are home to about 320 species of birds, Missouri has 403 species, Costa Rica has 857, and the rain forests of Colombia contain an astonishing 1,871. Other vertebrates follow this trend *(Figure 8.5)*.

Figure 8.5—Species richness tends to increase toward the equator.
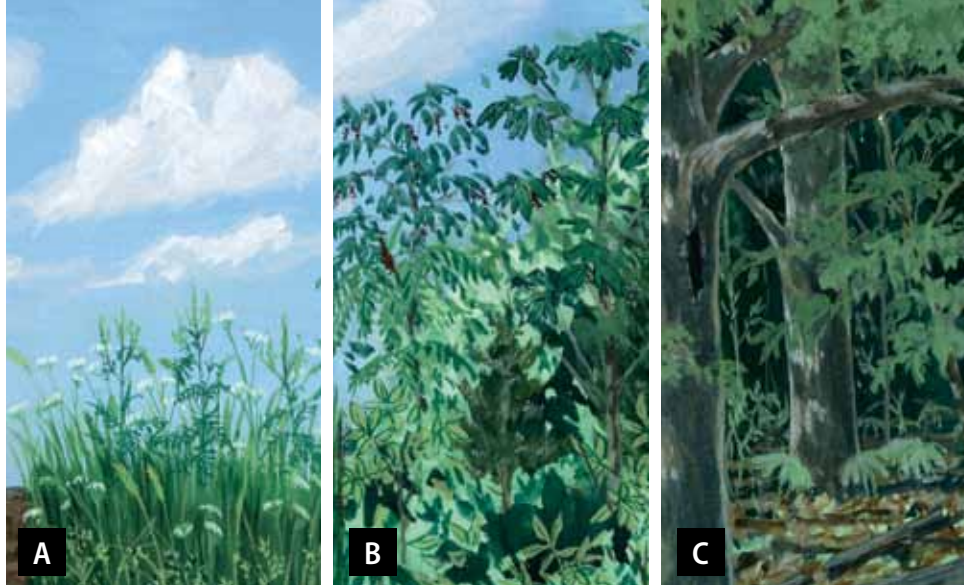
Mammals — Birds — Reptiles — Amphibians — Fish
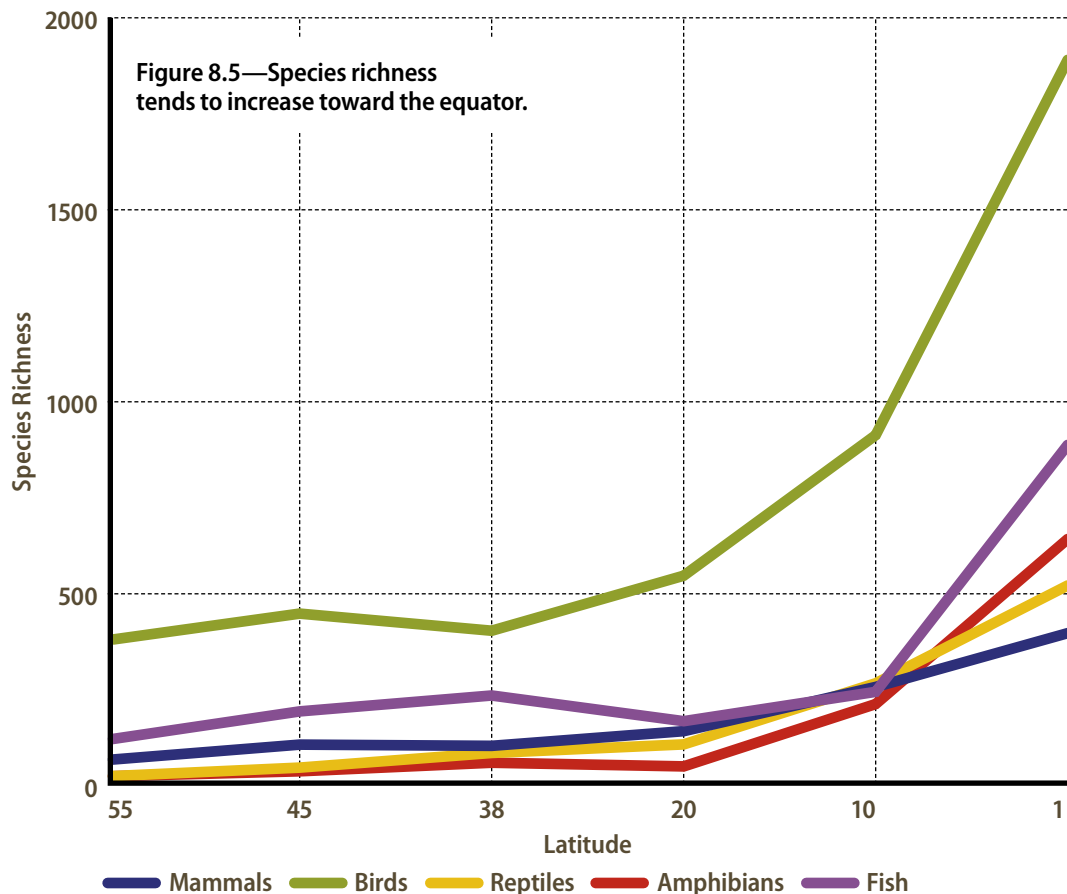
Figure 8.6—Ecosystems with more vertical layers of vegetation harbor a greater diversity of birds. Prairies (A), with a single layer of vegetation, contain fewer bird species than shrubby fields (B), which have two vegetation layers. Likewise, shrubby fields contain fewer species than forests (C), which have three vegetation layers.

Another interesting pattern is that biodiversity is higher in complex ecosystems compared to simple ecosystems. Robert and John MacArthur compared bird diversity in different habitats, including grasslands, shrubby fields and deciduous forests. The ecologists found that habitats with more vertical layers of vegetation contained a greater diversity of birds. For example, prairies, which have a single vegetation layer, contain fewer bird species than deciduous forests, which have ground, understory and canopy vegetation layers (Figure 8.6). They reasoned that more layers of vegetation provide more niches for a greater diversity of species. This relationship holds up for a number of different organisms and habitats. Coral reefs, for example, have a complex structure that supports far more fish species than the open ocean, which is structurally simple.

As a general rule, large areas harbor more species than small areas. In 1921, the botanist Olaf Arrhenius quantified this relationship, which ecologists call the **species-area rule**. Since that time, ecologists have collected evidence to strengthen the species-area relationship. Many have examined the relationship between species richness and the size of islands in the ocean *(Figure 8.7)*. They found that relatively few species live on small islands while many more species live on larger islands. The species-area rule holds true not only for islands in the ocean, but also for islands of habitat, such as a forest surrounded by subdivisions or a lake surrounded by miles of dry land.

In contrast, a negative relationship often exists between an island's species richness and the distance it is from similar blocks of habitat. Islands that are isolated usually support fewer species than islands that are in close proximity to other islands. This relationship puzzled ecologists until the 1960s.
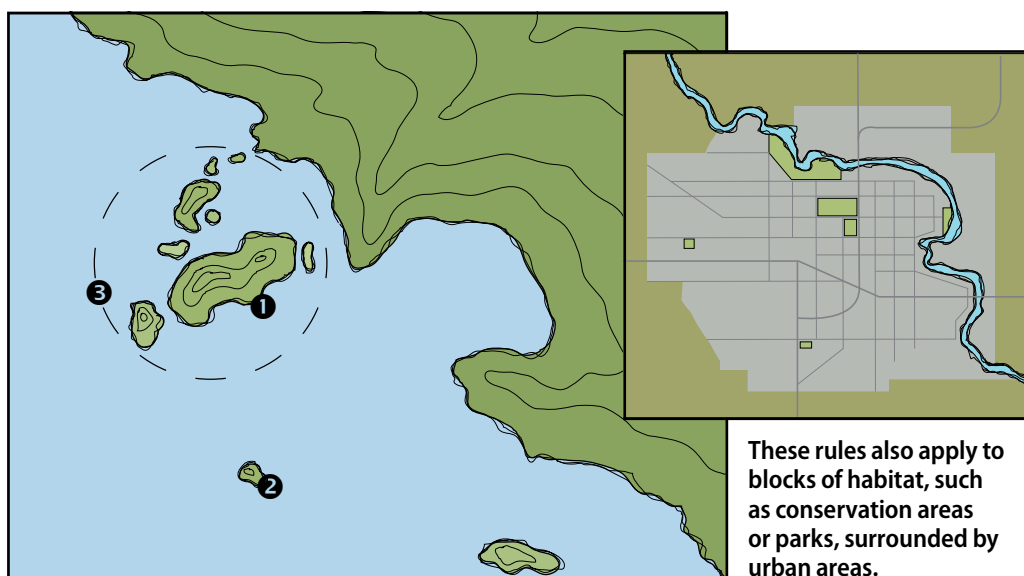

Figure 8.7—As a general rule, larger islands (1) support more species than smaller islands (2), and islands that are isolated (2) have fewer species than islands in close proximity to other islands (3).

These rules also apply to blocks of habitat, such as conservation areas or parks, surrounded by urban areas.

Missouri's Biodiversity Hotspots

Humans are the ultimate keystone species. Our actions, both intentional and otherwise, profoundly affect ecosystems. We encourage and protect species we like, such as white-tailed deer, largemouth bass, purple coneflowers and white oaks. These organisms provide us with food, building materials and other economic resources, or they are simply pretty and fun to watch. But what about species we don't like or species that escape our attention because they are too small, too secretive or they inhabit places too remote? As we've learned throughout this book, these species also play a role in biological communities.
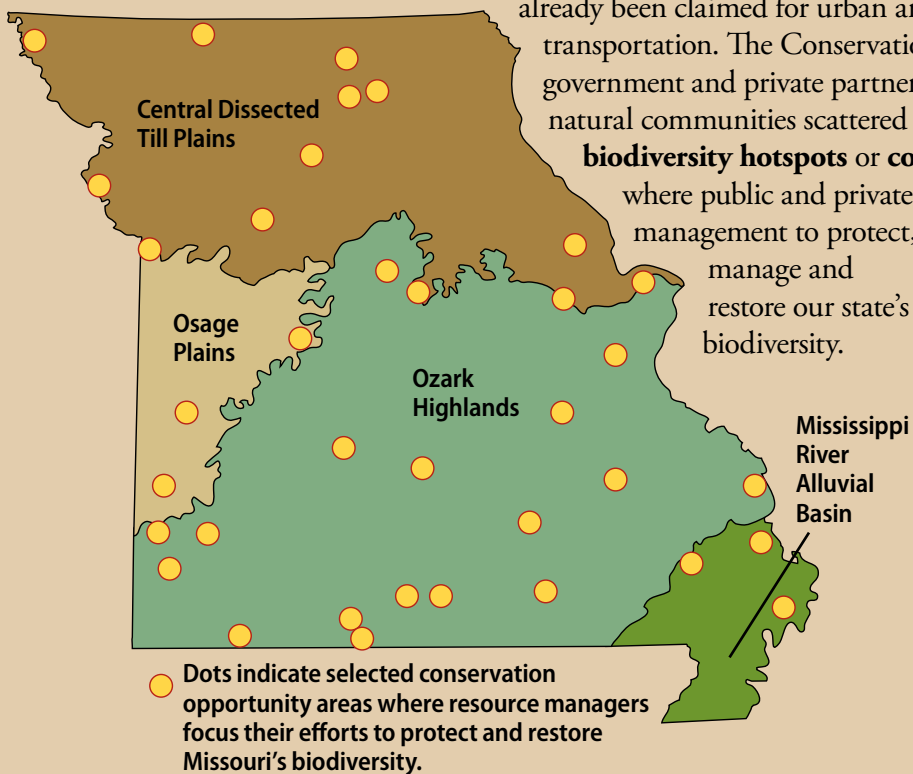
Traditionally, resource managers focused their efforts on specific species. Wildlife biologists managed habitats to increase populations of white-tailed deer, turkeys and other game animals. Foresters managed forests to increase yields of marketable trees for lumber, paper and other wood products. Fisheries biologists focused their efforts on fish anglers liked to catch. Management that focuses on specific species is called **featured-species management**.

In some cases, featured species management is still used. It's an important tool to maintain abundant, healthy populations of game animals and economically valuable plants. It's also critical to restore populations of rare and endangered organisms. In most cases, however, today's resource managers implement **community management**, focusing on entire biological communities rather than a few select species. Community management embraces the idea that all organisms are interconnected and interact within a community. As such, managers focus on nurturing conditions that maintain a community's structure and function. This may involve setting controlled fires to keep trees out of prairies, cleaning up streams, pumping water onto a wetland, or harvesting trees to mimic natural events such as forest fires and wind storms.

Ecologists divide Missouri into four large ecological regions. The Ozark Highlands is a region of forests, woodlands and glades cut by clear, spring-fed streams. Although now mostly farmland, the northern plains were formerly prairies and savannas dissected with wooded, muddy streams. The western border of Missouri lies at the edge of the Great Plains and represents our best remaining prairie communities. A century ago, Missouri's Bootheel was swampy and forested.

Not all locations within these regions are suitable for community management. Much land has already been claimed for urban areas, living space, food production and transportation. The Conservation Department, working with many government and private partners, has identified healthy, functioning natural communities scattered throughout each ecological region. These **biodiversity hotspots** or **conservation opportunity areas** are places where public and private conservation groups can use community management to protect, manage and restore our state's biodiversity.

Central Dissected Till Plains

Osage Plains

Ozark Highlands

Mississippi River Alluvial Basin

Dots indicate selected conservation opportunity areas where resource managers focus their efforts to protect and restore Missouri's biodiversity.

Foresters manage Missouri's forest communities for a variety of things, including lumber.

The species richness of a community is a balance between immigration and extirpation.

How do we explain patterns of diversity? Why do some communities contain more species than others? What ecological processes might increase or decrease species richness? In the 1960s, Robert MacArthur and E.O. Wilson developed a now famous model to help answer these questions. They called it the **equilibrium model of island biogeography**.

MacArthur and Wilson proposed that species richness is a balancing act between immigration of new species into a community and extirpation of existing species from a community. Consider a forest in which we have experimentally removed every single bird. When we allow birds back into the forest, the rate of immigration will, at first, be extremely high, since every bird that immigrates into our forest will likely be a new species. As more and more birds show up, however, the immigration rate will go down because fewer and fewer arrivals will be new species *(Figure 8.8)*. In addition, as more birds show up, competition between species will increase. Some species will likely outcompete others, leading to competitive exclusion. Thus, as species richness increases, extirpation rates increase also *(Figure 8.9)*.

Figure 8.8—As species richness increases, the number of new species that turn up will decrease.
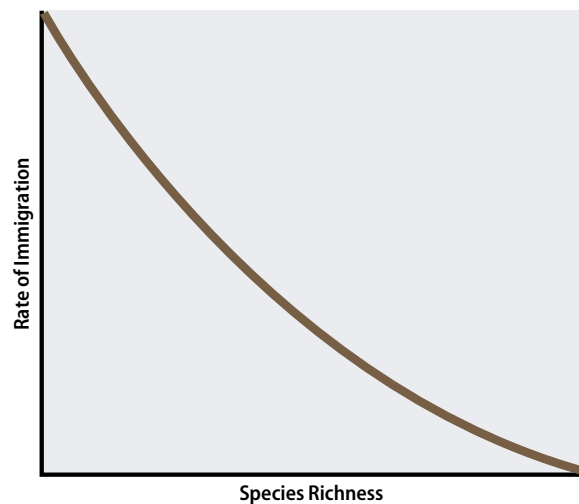

Figure 8.9—As species richness increases, the rate of extirpation also increases because more species are competing for the same resources.

Figure 8.10—At the equilibrium point, the number of new species immigrating to an island is balanced by the number of species extirpated from the island.
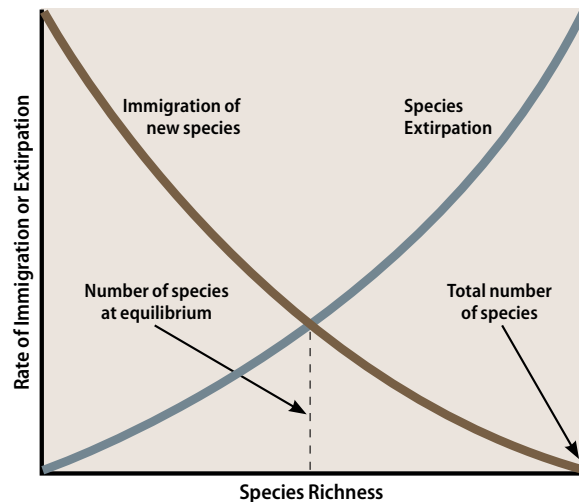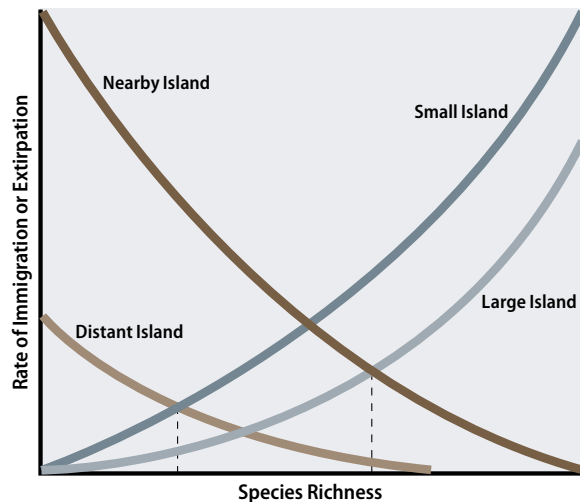

Figure 8.11—Small, distant islands have less species richness than large, nearby islands.

If you compare the two graphs, you'll notice that as species richness increases, the immigration rate falls and the extirpation rate rises. If we lay the two graphs over each other, the immigration rate and extirpation rate cross *(Figure 8.10)*. MacArthur and Wilson reasoned that the point where the two lines cross predicts the number of bird species that will occur in the forest. They called this the **equilibrium point** because at this level of species richness, the rate of immigration is balanced by the rate of extirpation.

MacArthur and Wilson proposed that a habitat's immigration rate is influenced mainly by its distance from a potential source of immigrants. Islands or blocks of habitat that are far from other blocks of similar habitat have lower immigration rates. Islands or blocks of habitat that are close to similar blocks of habitat have higher immigration rates. In contrast, MacArthur and Wilson proposed that an island's size is what mainly influences the rate of extirpation. They predicted that extirpation rates will be highest on small islands (or blocks of habitat) where resources are scarce and lowest on large islands where resources are plentiful. Thus, according to the equilibrium model of island biogeography, small, distant islands will have less species richness than large, nearby islands *(Figure 8.11)*.

Communities undergo a sequence of predictable changes following a disturbance.

To the casual observer, nothing seems to change in a community. A forest seems filled with the same oak trees and gray squirrels that were there last year or even 20 years before. Although some organisms die and others are born, oaks typically replace oaks and squirrels replace squirrels. A careful observer, however, will notice that communities are dynamic. When a community is disturbed—a forest logged, a prairie plowed, a marsh flooded—it changes in startling ways.

Imagine the Ozarks a hundred years ago. Both the Revolutionary and American Civil wars took a toll on our young democracy, and in the late 1800s the United States was struggling to rebuild. To do so, we needed lumber. To get it, logging companies flocked to the Ozarks. Clear Ozark streams became choked with sediment and long rafts of logged trees. Lumberjacks stood precariously atop the rafts, guiding them downstream to Grandin, a huge sawmill that needed about 30 hectares of trees *per day* to stay in business. To feed Grandin and other mills, hundreds of square kilometers of forests were recklessly logged. Eventually the trees ran out, the mills shut down, and the Ozark hills were left barren, with only a few tangles of briars hugging the rocky soil.

Following the lumber boom, the Ozark forests slowly rebuilt. Annual plants, such as ragweed and sunflowers, began growing almost before the last tree fell. Perennials, such as grasses and asters, sprang up the following year. Five years later, woody shrubs, such as blackberry and sumac, covered the hillsides. Within 20 years, young oaks and hickories formed dense thickets. And, in 70 to 100 years those trees had grown into the mature forests we see today.

During the logging boom in the late 1800s, Grandin sawmill in southern Missouri processed 30 hectares of trees daily.

This sequence of changes is called **succession**, or the replacement of one biological community by another over time. Ecologists recognize two types of succession. **Primary succession** begins on areas without soil, such as bare rock, lava flows and areas scraped lifeless by retreating glaciers. **Secondary succession** occurs when the preceding community is destroyed, but the soil is not. This kind of succession occurs after a farmed field is abandoned or a forest is logged.

Ecological disturbances cause secondary succession. **Disturbance**, to an ecologist, involves a departure from the typical environmental conditions of a community. There are many potential sources of disturbance. Abiotic forces, such as fires, tornadoes, ice storms and floods, create disturbance. Biotic factors, such as disease, pest outbreaks, predation and human activities, also can result in disturbance.

After a disturbance, the first species to show up form the **pioneer** or **early successional community**. Ragweed, crabgrass and most other weeds are often first to arrive. Their seeds, blown in on the wind or carried by animals, germinate and start to grow. By being the first to colonize a new habitat and by growing quickly, pioneer species often inhibit the growth of other species. Their dominance, however, is usually short-lived. Pioneer species gradually change the biotic and abiotic environment in which they live. Plants, for example, create shade, redistribute nutrients, alter moisture levels, and hold the soil in place. The changes pioneer species make often cause the environment to be less suitable for their own existence. These changes, however, create favorable conditions for the next successional stage of species. This happens over and over, each successional stage paving the way for the next, until succession ends with a **climax community**. Climax communities remain unchanged until they are destroyed by disturbance, at which point succession begins again.

Until this point, we've considered succession as a sequence of changes in the plant community of a disturbed area. We must remember, however, that succession also brings changes in the animal, fungal and microbial communities. Following logging, early successional animals, such as quail, indigo buntings and cottontail rabbits, were gradually replaced as the forest matured by late successional species, such as wood thrushes, pileated woodpeckers and flying squirrels *(Figure 8.12)*. Why? Early successional animals are adapted to the habitat created by early successional plants; late successional animals are adapted to the habitat created by late successional plants.

The frequency and intensity of disturbance affects a community's biodiversity. Frequent and intense disturbances tend to lower biodiversity, because only those species that can quickly recolonize and reproduce can survive the ever-changing conditions. Likewise, if disturbances are infrequent or of low intensity, biodiversity tends to be low because only species that can outcompete others survive. Biodiversity, then, is generally highest when disturbance is moderately frequent and moderately intense.

Early and late successional species have different adaptations.

What's the difference between ragweed and a red oak? If we examine each plant's physical appearance, we would say that the weed is low-growing, while the tree is tall. We would notice that ragweed is herbaceous while the oak is woody. Upon closer inspection, we might observe that ragweed, for its size, has an enormous number of tiny seeds. For its part, the oak has bigger seeds, but relatively few if we account for the tree's enormous size. If we were to plant both seeds and track their growth, we would learn that ragweed almost leaps out of the ground, while the oak grows s-l-o-w-l-y. The ragweed is, of course, a pioneer species and the oak a climax species. The tortoise-and-hare nature of how these plants disperse, grow and reproduce paints a picture of the different adaptations displayed by early and late successional species.

Early successional species disperse easily and quickly. They accomplish this by producing many small seeds that can be carried by wind or water. In addition, seeds of early successional species can remain dormant in the soil for years until a disturbance creates the bare-soil conditions required for germination. Early successional species germinate, grow and reproduce quickly. Because they often accomplish this in a single growing season, early successional species rarely reach towering heights or put on the woody tissues of longer-lived species. Their objective is to reproduce as quickly as possible before environmental conditions change.
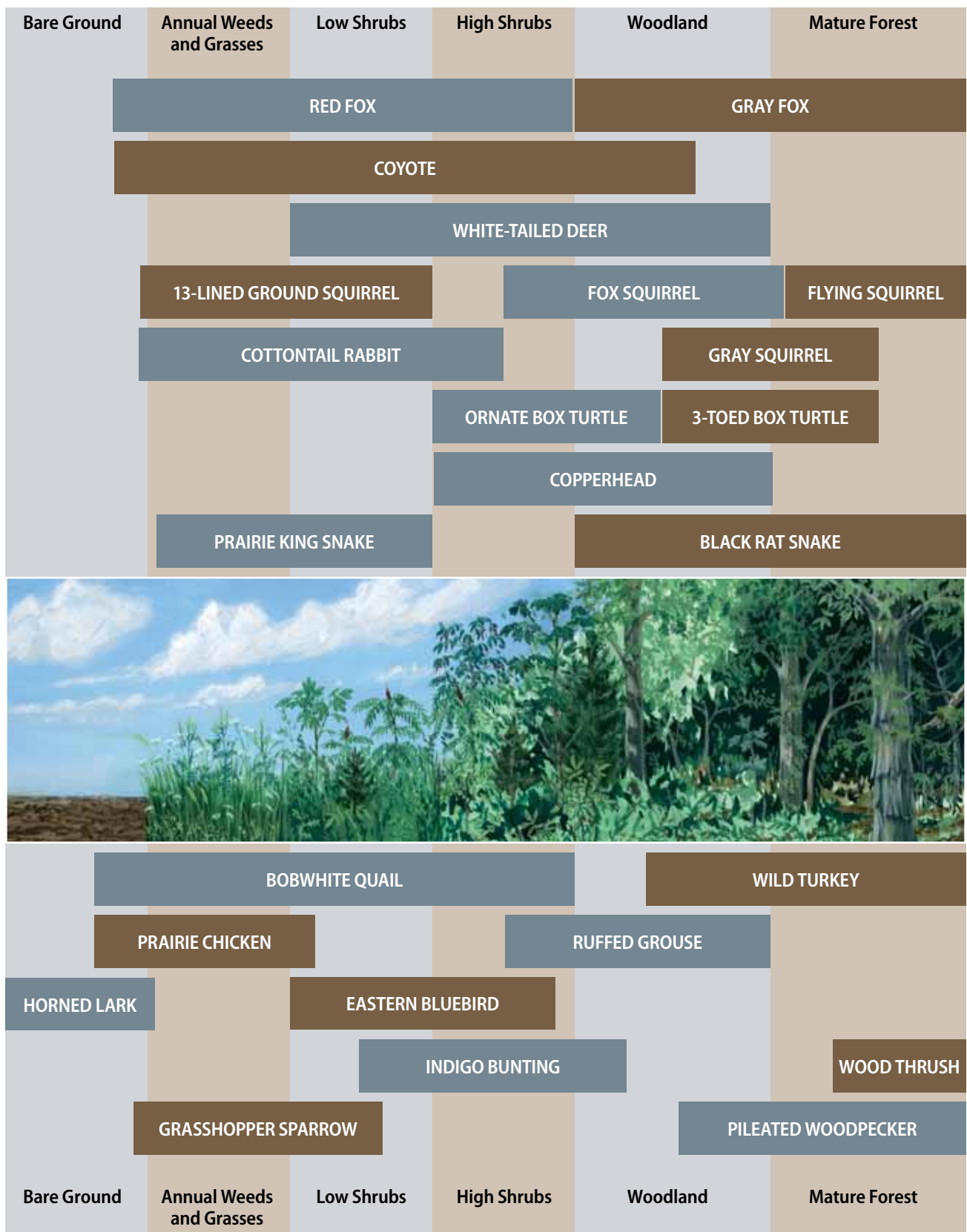
Figure 8.12—As succession progresses, the plant and animal species in a community change.

Characteristic	Early Successional Plant	Late Successional Plant
Number of seeds	many	few
Seed size	small	large
Dispersal	wind, water, stuck to animals	gravity, eaten by animals
Seed viability	long, survives in seed bank	short
Growth rate	rapid	slow
Mature size	small	large
Shade tolerance	low	high

Table 8.3—A Comparison of Early and Late Successional Plants

Ragweed is an early successional species, while an oak tree is a late successional species.

In contrast, the seeds of late successional species are relatively large. This provides their seedlings with plenty of nutrients to start growing in the shady, competitive conditions of the forest floor. Late successional species grow slower than early successional species because they allocate more growth to their roots and stems. This gives them a competitive advantage in the long run. With an abundance of roots to gather water and nutrients, and a towering stem to put leaves closer to sunlight, late successional species eventually outcompete early successional species for water, nutrients and sunlight. Thus, succession is accompanied by a shift from adaptations that promote dispersal, fast growth and reproduction to adaptations that enhance an organism's ability to compete for scarce resources. Table 8.3 compares the characteristics of early and late successional plants. ▲

Setting Back Succession

How do you keep a prairie full of grass? One of the best ways is to set it on fire.

Missouri is at the crossroads of two of North America's largest biomes, the eastern deciduous forest and the tallgrass prairie of the plains. The line between these two biomes divides Missouri almost in half, with prairie communities dominating the north half of the state, and forest communities dominating the south half of the state. This forest-prairie edge shifts based on rainfall and fire frequency. Missouri typically averages 96 centimeters of rainfall per year. Without periodic fires, trees advance into a prairie and shade out grasses and wildflowers. During a drought, however, fires can kill hardwood seedlings and open up areas so grasses can grow. You might say that in the case of prairies, disturbance maintains the climax community of grasses, while with forests, fires and other disturbances initiate succession.

In the past, Native Americans played a role in keeping grasslands open by purposely setting fires from time to time. Today, resource managers set controlled fires to keep trees and shrubs out of grasslands. The reason fire benefits prairie plants and harms forest plants has to do with how the plants grow. Most prairie plants grow from underground roots and rhizomes, which are usually safe from fire. In contrast, most forest plants grow from the tips of their stems and branches, which are often damaged by fire.

Managers boost biodiversity on prairies by setting fires at different times of the year. Burns in late winter or late summer favor wildflowers, cool-season grasses and woody shrubs. Burns in April and May favor warm-season grasses and help control woody plants.

Periodic fires are good for wildlife, too. By stimulating plant diversity, fire provides more food, shelter and nesting areas for animals. Fire removes plant litter on the ground making it easier for quail and other animals to move and find insects. And, fire creates bare areas where birds and small mammals take dust baths and reptiles and amphibians can warm up on cool days.

Resource managers use controlled fire to increase the biodiversity of prairies.